Effects of Elodea nuttallii on temperate freshwater plants, microalgae and invertebrates: small differences between invaded and uninvaded areas

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Effects of *Elodea nuttallii* on temperate freshwater plants, microalgae and invertebrates: small differences between invaded and uninvaded areas

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Abstract

The invasive aquatic plant species *Elodea nuttallii* could pose a considerable risk to European freshwater ecosystems based on its current distribution, rate of spread and potential for high biomass. However, little research has been conducted on the impacts of this species on native biota. This study takes an ecosystem-wide approach and examines the impact of *E. nuttallii* on selected physicochemical parameters (dissolved oxygen and pH), algae, invertebrate and macrophyte communities. *Elodea nuttallii* had small but significant impacts on plant, invertebrate and algal species. The richness of algal periphyton was lower on *E. nuttallii* than on native macrophytes. The taxonomic composition of invertebrate communities associated with *E. nuttallii* differed from that associated with similar native plant species, but did not differ in terms of total biomass or species richness. Macrophyte species richness and total cover were positively correlated with percentage cover of *E. nuttallii*. Not all macrophyte species responded in the same way to *E. nuttallii* invasion; cover of the low-growing species *Elodea canadensis* and charophytes was negatively correlated with *E. nuttallii* cover, whilst floating-rooted plants were positively correlated with E. nuttallii cover. All observed differences in the macrophyte community were small relative to other factors such as nutrient levels, inter-annual variation and differences between sites. Despite this, the observed negative association between *E. nuttallii* and charophytes is a key concern due to the rarity and endangered status of many charophyte species.

Introduction

Freshwater systems have been shown to be at particularly high risk from biological invasions (Sala et al. 2000) and invasive aquatic plants are widely considered to be a major threat to both species diversity and ecosystem functioning (Strayer 2010). The assessment of potential impacts of invasive species on ecosystems is essential to the prioritisation of resources (Leung et al. 2012), and traits associated with successful naturalisation cannot be reliably used to infer potential impact (Hulme 2012). Despite this, in Europe there is a lack of studies directly assessing the impacts of aquatic species on natural ecosystems across trophic levels (Caffrey et al. 2014).

Invasive macrophytes can be 'ecosystem engineers', fundamentally altering ecosystems through alterations to habitat structure and water chemistry (Strayer et al. 2010). The impacts of invasive macrophytes on native macrophytes are more frequently studied than their impacts on algae or invertebrates (Evangelista et al. 2014). Invasive macrophytes are frequently observed to be dominant in plant assemblages. They may reduce overall macrophyte richness (Carniatto et al. 2013; Michelan et al. 2010; Stiers et al. 2011) and native seed banks (de Winton & Clayton, 1996), and alter plant community composition (Mjelde et al. 2012; O'Hare et al. 2012). However, invasive macrophytes may benefit native plant species by altering the physical environment (e.g. stabilisation of sediment, reduction of turbidity or altering water clarity; (Rybicki, Landwehr 2007; Thomaz et al. 2012). Previous laboratory experiments conducted with *Elodea nuttallii* have shown that it can out-compete other submerged species (Barrat-Segretain 2005) and floating species when nutrient concentrations are not limiting (Szabo et al. 2010). However, floating species are likely to out-compete *E. nuttallii* in high nutrient conditions due to their superior ability to compete for light (Netten et al. 2010; Szabo et al. 2010).

Algal periphyton is a key link between macrophytes and aquatic invertebrate species (Hamilton et al. 1992). Algal periphyton communities differ between plant hosts (Toporoska et al. 2008) both as a result of plant architecture (Declerck et al. 2007; Warfe, Barmuta 2006) and chemical exudates (Erhard and Gross 2006). Suppression of algal taxa by macrophyte exudates has been observed for several submersed species, including *E. nuttallii* and its congener *Elodea canadensis* (van Donk 2002; Wu et al. 2009). As competition with periphyton and phytoplankton is a major limiting factor for aquatic macrophytes, such allelopathy could constitute a substantial competitive advantage for these species.

Allelopathic exudates may also affect zooplankton and macroinvertebrates, e.g. negative effects of *Elodea* spp. on growth and development of *Daphnia* spp. (Burks et al. 2000) and lepidopteran larvae in the family Pyralidae (Erhard et al. 2007). Many macrophyte species contain chemicals that deter grazing, and invertebrates and fish may preferentially select native macrophyte species as food (Burks, Lodge 2002; Schultz, Dibble 2012). Furthermore, the physical structure of different macrophytes provides different quality of refuges from predation (Kovalenko, Dibble 2014; Valinoti et al. 2011). In some cases, the increase in plant biomass associated with invasive macrophytes may increase the overall productivity of the invaded system, resulting in an increase in biomass and diversity of invertebrate species and changes in invertebrate community composition (Schultz, Dibble 2012).

Elodea nuttallii is a submerged freshwater plant species which occurs in lakes and slow moving rivers, and which could pose a significant risk to European waterbodies based on its rapid spread and high abundance (Champion et al. 2010) and the observed impacts of *E. canadensis*. Whilst spread rates and suitability of European waterbodies for the establishment of *E. nuttallii* have been studied (Hussner 2012; Kelly et al. 2014a; Kelly et al. 2014b), little research has been conducted on the impacts of this species in invaded waterbodies.

E. nuttallii was first introduced to Europe in 1939 and has spread rapidly, replacing the ecologically similar *E. canadensis* in many locations (Thiébaut et al. 2008). *E. canadensis* is considered to be one of the '100 worst' invasive species in Europe (DAISIE, 2015) and has impacts on macrophyte communities and aquatic food webs (e.g. deWinton, Clayton 1996; Kelly, Hawes 2005; Kornijow et al. 2005). *E. nuttallii* and *E. canadensis* are so similar that they may be ecologically and functionally redundant (Hérault et al. 2008), in which case their distribution and impacts could be expected to be similar. Both *E. canadensis* and *E. nuttallii* have high photosynthetic rates, show strong effects on pH, dissolved oxygen and CO_2 levels within plant stands (James et al. 1999) and may play an important role in phosphorus cycling in eutrophic systems (Angelstein, Schubert 2008). Field evidence suggests that *E. nuttallii* is replacing *E. canadensis* (Barrat-Segretain et al. 2001; Barrat-Segretain, 2002) and laboratory experiments have shown that *E. nuttallii* is more competitive than *E. candensis* (Barrat-Segretain 2005). Hence, the impacts of *E. nuttallii* could be more severe than those of *E. canadensis*.

According to the "invasion meltdown" hypothesis (Simberloff 2006) invasive species may facilitate the establishment or growth of other invasive species leading to accelerating rates of invasion; however, there are few empirical examples (Montgomery et al. 2012). Recent research on invasive macrophytes found evidence of facilitation of *Egeria densa* by *Ludwigia grandiflora*, but mutual inhibition between *Ludwigia grandiflora* and *Myriophyllum aquaticum* (Thouvenot et al. 2013), suggesting that such interactions may be species- and/or context-specific. Therefore, it is important to examine the potential interactions between *E. canadensis* and *E. nuttallii* where they co-occur in order to ascertain whether impacts on native biota are amplified by the interaction of these species.

Here, we describe two correlational studies which provide insights into the potential impacts of *Elodea*. Firstly, we used historical data on the macrophyte communities in two

large lakes over the course of an invasion to examine the impact of *E. nuttallii* on other macrophyte species, and to examine interactions between *E. nuttallii* and *E. canadensis*. Secondly, we used a paired survey design to examine differences in micro-algae and invertebrates associated with native macrophytes and invasive *E. nuttallii* within six waterbodies. We used a combination of standard community metrics (e.g. biomass and species richness) and multivariate analysis of communities, both in terms of taxonomic groups and broader functional or structural groups, to examine impacts at different trophic levels.

Methods

Macrophyte study sites

Lough Erne in County Fermanagh, Northern Ireland, comprises Upper Lough Erne (*ca*. 29 km^2) and Lower Lough Erne (*ca*. 104 km^2). Lough Erne is a naturally eutrophic lake system with high alkalinity due to the underlying geology of the area. Upper Lough Erne is the shallower of the two lakes with a mean depth of 2.9 m; Lower Lough Erne has a mean depth of 11.9 m. Over the period of this study pH in these lakes ranged from 6.2 to 9.3, total phosphorus from 10 μg l^{-1} to 780 μg l^{-1} and nitrates from 20 μg l^{-1} to 1,080 μg l^{-1} (data provided by Northern Ireland Environment Agency (NIEA), based on monthly measurements at ten monitoring points from 2006-2010). Lough Erne is notable for its conservation value, being designated as a Special Area of Conservation (SAC) and Ramsar site and containing many Irish Red Data List species, including the pointed stonewort (*Nitella mucronata*) and aquatic invertebrates such as the pond skater (*Limnoporus rufoscutellatus*), water beetles (*Donacia aquatica, D. bicolora, Gyrinus distinctus, G. natator* and *Hydroporus glabriusculus*) and white-clawed crayfish (*Austropotabius pallipes*). *E. nuttallii* was first recorded in Lough Erne in 2006.

Field and laboratory methods

Data on macrophyte community composition were obtained for both Upper and Lower Lough Erne from the Water Management Unit (WMU), NIEA. These data represent a total of 15 transects in Upper Lough Erne during 2007 and 2010 and 18 transects in Lower Lough Erne during 2006 and 2009. Surveys were carried out by wading and by boat depending on water depth. Macrophyte species and percentage cover were recorded within 5 m^2 quadrats positioned every 5 m along each transect perpendicular to the shoreline until the edge of the macrophyte zone was reached. Nitrogen and phosphorus (NO_3N, NO_2N, NH_4N, Total Organic Nitrogen, soluble P, and Total P) were measured in surface waters in late July or August for each survey year at a central point in Upper Lough Erne and two points in Lower Lough Erne (Fig 1). These chemistry data are included to account for differences between lakes and over time, rather than smaller scale differences between transects. Unfortunately, it was not possible to obtain more detailed information on water chemistry due to the historical nature of the dataset. We have also accounted for this issue by using a paired statistical design which means that we are not comparing quadrats from different parts of the lakes. Only quadrats which were surveyed in both years were used in the analysis (n = 728 quadrats).

In order to determine whether the presence of *E. nuttallii* affected the structure of macrophyte beds, each macrophyte species was allocated to one of eight groups based on its structural characteristics: emergent, free-floating, floating rooted, submerged (canopy forming), submerged (low growing), bryophytes, filamentous algae and charophytes.

Dissolved oxygen, pH, algae and invertebrate study sites

A paired survey design of six sites in Northern Ireland was used to examine the associations between *E. nuttallii*, dissolved oxygen, pH, and algal and invertebrate communities, between

July and September 2010 (Fig 2.). At each site a native macrophyte stand and a stand of the invader were chosen within the same water body (distance between macrophyte stands <500 m). Native species differed between sites, but all had a predominantly submerged habit. Native species and sites were as follows: *Potamogeton pectinatus* (Lagan), *Potamogeton perfoliatus/Myriophyllum spicatum* (Ballyronan), *Potamogeton natans* (Lough Cashel), *Ceratophyllum demersum* (Loughbrickland and Upper Bann), *Sagittaria sagittifolia* (Lower Bann). Waterbodies were selected to represent the most common site conditions in which *Elodea nuttallii* was found and included three lake sites and three slow-flowing river sites. All samples were taken in shallow water between 0.45 m and 1.05 m in depth. There was no consistent pattern as to whether *E. nuttallii* or native plants occurred in deeper water (the mean difference in depth between *E. nuttallii* and native plants within sites was 14 cm). Sites covered a range of nutrient levels from mesotrophic to hypereutrophic (measured total phosphorus ranging from 18 μg l^{-1} to 1,168 μg l^{-1} and total dissolved nitrogen between 4.61 μg l^{-1} and 530 μg l^{-1}).

Field and laboratory methods

Water chemistry, environmental data and algal sampling took place monthly for 3 months from July to September 2010. The pH and dissolved oxygen were recorded at each site using a Hanna pHep 4 pH meter and a portable dissolved oxygen meter (VWR DO200). Two litres of water was collected within each macrophyte bed for chlorophyll *a* analysis, filtered using a 0.45 μm Metricel® membrane filter and stored at -20°C. Chlorophyll *a* analysis was conducted using methanol-based pigment extraction and spectrophotometry readings (Hamilton, 2010). A further two litres of water was collected for nutrient analyses: soluble reactive phosphorus (SRP), total phosphorus (TP), total soluble phosphorus (TSP), total organic nitrogen (TON), ammonium (NH_4), nitrogen dioxide (NO_2), nitrates (NO_3) and total

dissolved nitrogen (TDN). Nutrient analyses were conducted by the Agri-Food and Biosciences Institute, Newforge Lane, Belfast, Northern Ireland.

Algal periphyton was collected by taking approximately 10 cm length of plant material from both the tip and the base of the macrophyte with approximately 15 ml of water immediately surrounding the macrophyte leaves. Care was taken to carry out this procedure slowly and carefully *in situ* to minimise loss of periphyton. Water samples were filtered through a 250 μm mesh within 10 minutes of sampling to remove zooplankton and preserved using Lugol's Iodine solution (5 g iodine (I_2), 10 g potassium iodide (KI), 85 ml distilled H_2O). One algal sample was taken in each invaded and each uninvaded macrophyte bed in each of July, August and September. Algal samples were kept in the dark at 5-7 °C before processing.

Algal periphyton was separated from plant samples by vigorous shaking for 60 seconds. The algal sample was then transferred into a sterile 20 ml tube. Plant material was dried at 60°C for 72 hrs and the dry mass was recorded. The algal sample was placed in a Lund chamber. Five horizontal transects of the chamber were carried out at x100 magnification and larger species were identified and counted. A further 20 random fields of view (450 μm^2) were examined at x400 magnification and all species were identified and counted. Taxa were identified to genus level where possible, or to the lowest practical taxonomic level (Bellinger, Sigee 2010; Cox 1996; John et al. 2002). It was not possible to accurately identify all cells under 10 μm; those which could not be identified were measured for biovolume and recorded as "unidentified genera" (1.9% of total algal biovolume). For unicellular and colonial algae, the first 10 cells or colonies of each genus or species were measured. For filamentous algae, the first 30 filaments were measured as there was greater variation observed in filament length than in cell or colony size. Mean cell biovolumes were calculated

using the 'WISER phytoplankton counter spreadsheet' (Carvalho et al. 2007) and biovolume formulae were added for new taxa as defined in Hillebrand et al. (1999).

Algal species were categorised into seven functional groups based on Kruk et al. (2010) plus an eighth group of 'uncategorised genera' (Supplementary Material, Table S1). These groups have been proposed to be useful predictors of algal responses to environmental variables as they are closely linked with functional characteristics such as prey avoidance, *K* and *r* strategies and sinking rates (Kruk et al. 2010).

Invertebrates were sampled during July and late September/early October using two methods at each sampling date. Firstly, at each site, four replicate core samples of sediment were taken from each macrophyte bed using a KC Denmark Kayak core sampler 45 mm in diameter (hereafter, referred to as 'sediment invertebrate samples'). Secondly, invertebrates present in macrophyte material were collected using a bespoke bucket and mesh trap of 379 cm^2 surface area and 300 μm mesh size (hereafter, referred to as 'macrophyte invertebrate samples').

Invertebrates were separated from samples using a 250 μm sieve and stored in 70% ethanol. Plant material was dried at 60° C for 72 hrs and its dry mass recorded for calculation of macrophyte stand density. All invertebrates were identified to the lowest possible taxonomic level (Edington, Hildrew 1995; Elliott, Mann 1998; Fitter, Manuel 1986; Friday 1998; Gledhill et al. 1993; Savage 1989; Wallace et al. 1990). For sediment invertebrate samples, specimen length, width and dry mass were measured (n = 523). Linear regressions based on the length or width and biomass (transformed by Log_{10} or a natural logarithm depending on best fit described by the adjusted R^2 value) were conducted using SigmaPlot 10 to describe the relationship between individual length/width and biomass for each common invertebrate family or genus (Supplementary Material, Table S2). In taxa that exhibited a significant relationship between length/width and body mass these regression formulae were

used to calculate the biomass of individuals of that taxa in the macrophyte invertebrate samples. For all other species dry mass was measured directly. Invertebrate species were further categorised into six functional feeding guilds: collector filterers, collector gatherers, herbivore piercers, predators, scraper grazers and shredders following (Chaloner et al. 2009; Compin, Cereghino 2007; Cummins, Klug 1979; Heino 2008) (Supplementary Material, Table S3).

Statistical analyses

Macrophytes

In Lough Erne, the impact of *Elodea* spp. on total macrophyte cover, non-*Elodea* macrophyte cover and species richness (i.e. native plants) was examined using a Generalized Linear Mixed Model (GLMM) approach. Explanatory variables in the models were Year (fitted as a factor with four levels: 2006, 2007, 2009 or 2010), water depth and nutrient concentration, the percentage cover of *E. nuttallii*, the percentage cover of *E. canadensis*, and the interaction of *E. nuttallii* and *E. canadensis.* Nutrient concentration was expressed as the first axis of a PCA analysis of nitrogen and phosphorus values, which explained 62.7 % of the variance with a positive relationship with nitrogen variables (r = 0.95) and a negative relationship with phosphorus variables (r = -0.67). Quadrat nested within lake was included as a random factor.

All GLMMs were first fitted with a Gaussian distribution and identity link function. Model residuals were tested for normality using a Shapiro-Wilk test. Models for which residuals were not normally distributed were refitted using alternative distributions more suited to the response data. Specifically, gamma distributions with a log-link function were used for continuous response data and a Poisson distribution with a log link function was

used for count data (i.e. species richness). In each GLMM, all possible subsets of explanatory variables were ranked using the Akaike Information Criterion adjusted for small sample sizes (AICc), and the most optimal model was taken as that with the lowest AICc value.

Multivariate responses in macrophyte communities were assessed using partial Canonical Correspondence Analysis (pCCA). Two pCCAs were conducted, the first with a response matrix of percentage cover of macrophyte structural groups and a second with percentage cover of macrophyte genera. The associated environmental matrix included the percentage cover of *E. nuttallii*, *E. canadensis*, Year (as a factor), water depth and nutrient content. Quadrat was fitted as a random factor. The optimal model was obtained following stepwise forward selection followed by backward stepwise elimination. Explanatory variables were sequentially added to a null model (with site fitted as a random factor) where these variables significantly improved model AICc values based on a permutation test ($P < 0.05$ for inclusion), and then successively dropped from the model based on the same inclusion criteria. As *E. canadensis* was not included in the final pCCA model, it was then added to the response matrices (i.e. plant genera and structural datasets).

In order to assess whether species communities where *E. nuttallii* was present were more similar to each other than those without *E. nuttallii*, an analysis was carried out on multivariate homogeneity of group dispersion using the function “betadisper” in R based on a Jaccard dissimilarity distance matrix. This was conducted based on a Jaccard dissimilarity distance between species communities (i.e. the proportion of species which differed between quadrats where *E. nuttallii* was present vs. the proportion of species which differed between quadrats where *E. nuttallii* was not present).

Dissolved oxygen, pH, algae and invertebrates

GLMMs were used to examine all univariate dependent variables in relation to the presence of *E. nuttallii*. Water chemistry response variables (dissolved O_2 saturation, pH and chlorophyll *a*) were tested for correlation prior to GLMM analysis using Spearman's rank correlation test. There was no significant correlation between these variables (dissolved O_2 – chlorophyll *a* (rho = 0.168, P = 0.327), dissolved O_2 – pH (rho = 0.286, P = 0.091) and chlorophyll *a* and pH (rho = 0.086, P = 0.617). Explanatory variables for these physiochemical variables were the presence or absence of *E. nuttallii* and month (July, August or September), waterbody type (i.e. two level factor "Lake" or "River") and the interaction between *E. nuttallii* presence and waterbody type. Site was fitted as a random factor.

Explanatory variables for GLMMs of algal biovolume, algal species richness and macrophyte bed density were the presence and absence of *E. nuttallii*, month, waterbody type (i.e. a two level factor "Lake" or "River") and the interaction between *E. nuttallii* presence and waterbody type, nutrient concentration and the interaction of *E. nuttallii* and nutrient concentration. Nutrient concentration was expressed as the first axis of a PCA analysis of nitrogen and phosphorus values which explained 64.1 % of the total variance and had a positive relationship with both nitrogen (r = 0.83) and phosphorus variables (r = 0.73). Site was fitted as a random factor.

Invertebrate richness and biomass in both macrophyte samples and sediment core samples were examined as above for algae. However, macrophyte bed density was added as an explanatory variable to each model. Model selection was as above for previous GLMMs.

Multivariate community responses were assessed using pCCA. Response matrices for algae were biovolume of each algal functional group and biovolume of each algal taxon (per unit of plant dry mass). Response matrices for invertebrate species were the biomass of

309 invertebrate feeding guilds and biomass of invertebrate taxa. The associated explanatory
310 environmental matrix included the same factors and covariates as those used in univariate
311 analyses i.e., the presence/absence of *E. nuttallii*, month and nutrient concentrations,
312 waterbody type and the interaction between *E. nuttallii* presence and waterbody type, with
313 the addition of plant density in invertebrate models only. Site was fitted as a random factor.
314 Model optimisation was conducted as previously described for pCCAs of macrophyte
315 communities.

316 In order to assess whether algal and invertebrate communities on *E. nuttallii* were more
317 similar to each other than those on native plants were to each other we conducted an analysis
318 of multivariate homogeneity of group dispersion using the function "betadisper" in R (as per
319 macrophyte community data).

320 Unless otherwise stated all analyses were performed using R 3.0.2 (R Core Development
321 Team 2012) and the packages glmmADMB (Fournier et al. 2012), MuMIn (Barton 2013)
322 and vegan (Oksanen et al. 2013).

323

324 ## Results

325

326 *Macrophytes*

327 *Elodea nuttallii* was present in 2% of the 728 quadrats in the initial survey in 2006-07 and
328 increased to presence in 70% of quadrats in 2009-10. Over the same period, the percentage
329 cover of *E. nuttallii* within each quadrat increased from a mean of 0.03% (0-4%) to 21.3%
330 (0-100%) on resurvey in 2009-10. *E. canadensis* declined in presence from 33% to 9% of
331 quadrats and in mean cover per quadrat from 1.1% (0%-70%) to 0.5% (0%-30%) over the
332 same period. A total of 71 other macrophyte species was recorded. *E. canadensis* and *E.*
333 *nuttallii* were the only invasive species recorded in these surveys.

Total macrophyte cover within quadrats was positively associated with cover of both *E. nuttallii* ($\beta = 0.013 \pm 0.003$, $\chi^2 = 20.24$, $P < 0.001$) and *E. canadensis* ($\beta = 0.029 \pm 0.012$, $\chi^2 = 5.53$, $P = 0.019$). Excluding both *Elodea* species from the total macrophyte cover, the cover of remaining species was not significantly associated with the cover of either *E. nuttallii* or *E. canadensis*, but declined with water depth and differed between years. Both total macrophyte cover and the cover of non-*Elodea* species were negatively associated with water depth, the PCA axis of nutrient concentration and differed between years (see Supplementary Material, Table S5).

Species richness of macrophytes other than *E. nuttallii* and *E. canadensis* (i.e. native species) was positively associated with percentage cover of both *E. nuttallii* ($\beta = 0.002 \pm 0.001$, $\chi^2 = 3.85$, $P = 0.050$) and *E. canadensis* ($\beta = 0.013 \pm 0.004$, $\chi^2 = 11.58$, $P < 0.001$) and with the PCA axis of nutrient concentrations and negatively associated with water depth and differed between years (see Supplementary Material, Table S5). There was no evidence of an interaction between *E. canadensis* and *E. nuttallii* in any model.

The pCCA of macrophyte structural groups showed that year and percentage cover of *E. nuttallii* influenced structural composition and explained 4.6% of the variation in plant structure after variation between quadrats (69%) was accounted for ($P < 0.005$; Fig. 3). The pCCA of macrophyte genera showed that water depth, year and percentage cover of *E. nuttallii* influenced composition of genera significantly and explained 3.9% of the variation after between-quadrat variation (53.9%) was accounted for ($P < 0.005$). The percentage cover of *E. nuttallii* alone (with the other factors accounted for by pCCA) explained only 0.6% and 0.5% of the variation in structural groups and genera respectively ($P < 0.033$ and $P < 0.005$ respectively; Supplementary Material, Table S6). The cover of submersed low-growing species and charophytes was negatively associated with the cover of *E. nuttallii*, whilst the surface-growing plants (both free-floating and rooted) were positively associated with *E.*

359 *nuttallii* (Table 1). At a taxonomic level, the most negatively affected species was *E.*
360 *canadensis* whilst *Nuphar lutea* and *Stratiotes aloides* were most positively associated (Table
361 2). However, variance in plant community explained by *E. nuttallii* was very low relative to
362 variance between quadrats and between years (Tables 1, 2).

363 Analysis of multivariate homogeneity of group dispersion showed that quadrats
364 containing *E. nuttallii* were more homogeneous (mean Jaccard dissimilarity = 0.43, s.e. <
365 0.01) than those that did not contain *E. nuttallii* (mean Jaccard dissimilarity = 0.49, s.e. <
366 0.01) ($F = 24.34$, $P < 0.001$).

367

368 *Dissolved oxygen, pH, algae and invertebrates*

369 Dissolved O_2 saturation differed between lakes and rivers being higher in lakes than in rivers.
370 The presence of *E. nuttallii* was included in the best model of dissolved O_2 saturation (χ^2 =
371 3.21, $P = 0.073$), being higher in *E. nuttallii* stands (mean ± s.e. = 93.97% ± 5.46) than in
372 native plant stands (85.13% ± 3.86). Chlorophyll *a* showed no significant association with
373 rivers or lakes, months or the presence of *E. nuttallii*. The pH varied significantly between
374 months, but was not significantly associated with the presence of *E. nuttallii* (Supplementary
375 Material, Table S7).

376 Macrophyte bed density did not differ between *E. nuttallii* and native macrophyte beds
377 and was not associated with any of the other variables tested. The optimal model for algal
378 species richness contained *E. nuttallii* with marginal significance ($\chi^2 = 3.67$, $P = 0.055$) and
379 month, but not nutrient concentration. Algal biovolume per gram of plant dry mass varied
380 significantly between months. Algal biovolume was not affected by either the presence of *E.*
381 *nuttallii* or nutrient concentration (Supplementary Material, Table S8).

382 The pCCA of algal community data showed no significant effect of *E. nuttallii* on algal
383 community composition in terms of either functional groups or taxa. The community

384 composition in terms of algal functional groups was not significantly associated with any of
385 the explanatory variables tested. However, nutrient concentration and month significantly
386 affected community composition in terms of algal taxa (P = 0.015). Analysis of multivariate
387 homogeneity of group dispersion did not show any significant difference in the variance
388 between algal communities on *E. nuttallii* and those on native plants (F = 0.42, P = 0.521).
389 None of the community metrics of invertebrate species on macrophytes or sediment
390 differed between *E. nuttallii* and native macrophyte samples. Invertebrate species richness,
391 derived from macrophyte samples, varied significantly between months. Invertebrate
392 biomass in macrophyte samples also varied significantly between months and was positively
393 correlated with plant density and nutrient concentration. Invertebrate species richness in
394 sediment cores was not significantly associated with any of the environmental parameters.
395 Invertebrate biomass in the sediment cores was positively associated with nutrient, but not
396 with any of the other environmental parameters (Supplementary Material, Table S9).
397 The pCCAs of invertebrate taxonomic communities sampled from macrophytes showed a
398 significant effect of the interaction of waterbody type and the presence of *E. nuttallii*,
399 suggesting that the impact of *E. nuttallii* on invertebrate communities differed between lakes
400 and rivers. This interaction explained 10% of the variation in invertebrate communities (P =
401 0.043) after variation between sites (45%) was accounted for (P = 0.005). When rivers and
402 lakes were examined separately, *E. nuttallii* was found to explain 9% of variation in
403 invertebrate communities in lakes and 13% of the variation in rivers, after accounting for
404 variation between sites (41% and 33% respectively; Tables 3 & 4, Fig. 3). The pCCAs of
405 invertebrate functional groups from the macrophyte invertebrate samples and the pCCAs of
406 invertebrate community in sediment core samples showed no association with any of the
407 tested variables after accounting for variation between sites (Supplementary Material, Table
408 S10). In addition, analysis of multivariate homogeneity of group dispersion did not show any

409 significant difference in the variance between invertebrate communities associated with *E.*
410 *nuttallii* stands and those associated with native plant stands in either macrophyte (F = 0.15,
411 P = 0.702) or sediment samples (F = 1.92, P = 0.179).
412

413 ## Discussion

414

415 Freshwater communities associated with *Elodea nuttallii* differed in small but significant
416 ways from uninvaded communities. Specifically, we observed differences in oxygen
417 saturation, plant and algal richness, and invertebrate and macrophyte species composition.
418 However, observed differences were small relative to other factors such as nutrient levels,
419 inter-annual variation and differences between sites. Furthermore, there was no evidence of
420 any effect of *E. nuttallii* on the biovolume of periphytic algae, biomass of invertebrate
421 species or the cover of native macrophyte species. In addition, whilst plant communities in
422 quadrats containing *E. nuttallii* were more similar to each other than quadrats in which *E.*
423 *nuttallii* was not present, no similar effect was observed on algal or invertebrate
424 communities.

425 The effects of *E. nuttallii* on species communities could be seen as both positive and
426 negative, for example, the increased species richness of macrophyte species may be
427 contrasted with the lower richness of algal taxa. Increases in floating plants associated with
428 *E. nuttallii* can be contrasted with declines in submerged species. The association between
429 floating plant species and *E. nuttallii* may arise as a result of structural complexity where *E.*
430 *nuttallii* reaches the water surface, which reduces surface turbidity and provides anchorage
431 for floating species. In addition, floating species are most likely to out-compete *E. nuttallii*
432 for light and have been shown to out-compete *E. nuttallii* in high nutrient conditions (Netten
433 et al. 2010; Szabo et al. 2010). Submerged species which are negatively associated include

low-growing species which are likely to be shaded by *E. nuttallii* (such as *Eleocharis acicularis, Isoetes spp., Littorella uniflora*), canopy-forming submerged species occupying a similar niche space to *E. nuttallii* (including *E. canadensis*) and charophyte species.

Although the observed negative association between *E. nuttallii* and charophytes is small, this is of concern due to the rarity and conservation status of charophyte species. Charophytes are usually low-growing (< 0.5 m in height) and are likely to be out-competed for light by *E. nuttallii*. While this negative association could arise in this study from charophytes reducing the likelihood of establishment of *E. nuttallii*, this seems unlikely as charophytes have been previously shown to be out-competed by structurally similar invaders from the same plant family (e.g. *Lagarosiphon major* (Barrs et al. 2008) and *E. canadensis* (Mjelde et al. 2012)).

The observed negative association between the cover of *E. nuttallii* and *E. canadensis* suggests a competitive interaction between these two closely related invasive species. We did not find any indication that *E. nuttallii* or *E. canadensis* interact to increase impacts on native macrophyte cover or richness. Therefore, our findings do not support the invasion meltdown hypothesis in the case of *E. nuttallii* and *E. canadensis*. In addition, the observed rapid increase range and abundance of *E. nuttallii* in Lough Erne (such that it is much now much more frequently observed than *E. canadensis*), supports the suggestion that *E. nuttallii* may be replacing *E. canadensis* in parts of its invaded range (Barrat-Segretain et al. 2001; Barrat-Segretain, 2002).

It is perhaps surprising that species richness of native macrophytes was positively associated with the presence of *E. nuttallii* and *E. canadensis* in Lough Erne, after differences in nutrient levels and between years had been accounted for. Mechanisms for facilitation of native plant species could include alteration of flow rate and turbidity, or increases in primary productivity over time through the release of nutrients from the sediment. However, these alterations could also make conditions suitable for further establishment of *E. nuttallii*, which

459 can absorb nutrients directly from the water column and is adapted to low-light conditions
460 (Angelstein, Schubert 2008, 2009). An alternative explanation for the positive correlation
461 between *E. nuttallii* and species richness of native macrophytes is that some other
462 environmental factor, unaccounted for here, facilitates both an increase in *E. nuttallii* cover/or
463 its establishment and macrophyte species richness. Previous studies have suggested that while
464 species richness increases resistance to invasion at small spatial scales (Kennedy et al. 2002),
465 such effects may be overwhelmed by environmental factors which co-vary with species
466 richness, such as propagule pressure, resulting in an apparent positive relationship between
467 invasive species and native species richness (Levine 2000; Lonsdale 1999). Furthermore, a
468 recent large-scale study of invasive species in macrophyte communities found no clear
469 relationship between native species richness and exotic species richness (Capers et al. 2007).
470 In common with previous authors we found that plant density was significantly correlated
471 with the biomass of invertebrate species living on macrophytes (Schultz, Dibble 2012).
472 However, in our study plant density and invertebrate biomass did not differ between *E.*
473 *nuttallii* and native plants, reflecting an explicit decision to examine differences between
474 similar native and invasive plant beds. Whilst *E. nuttallii* may not alter the biomass of
475 invertebrate species relative to similar-sized plants, results from our macrophyte dataset
476 suggest that *E. nuttallii* may be replacing low-growing species and increasing overall
477 macrophyte cover. Hence, by altering the relative regional abundance of different plant
478 functional groups, *E. nuttallii* may produce corresponding changes in invertebrate biomass at
479 larger spatial scales.
480 Differences in invertebrate assemblages associated with macrophytes have also been
481 shown previously for similar submerged invasive species (Hogsden et al. 2007; Kelly, Hawes
482 2005; Stiers et al. 2011). The reasons for the observed differences in invertebrate species
483 composition may be varied and complex, and are likely to relate to differences in plant

architecture, plant palatability, chemical exudates, water chemistry and water flow rates. Oxygen saturation is an important factor in determining invertebrate communities in freshwater environments. Higher oxygen saturation levels associated with *E. nuttallii* may have influenced species composition here: there was a lower abundance of some species groups associated with low oxygen saturation levels such as true fly larvae in the family Chironomidae, Alderflies (*Sialis lutaria*), leeches in the genera *Erpobdella* and *Theromyzon*, and *Asellus* amphipods, and a higher abundance of some species associated with higher oxygen saturation such as caddisflies in the family Linephiidae. However, several species behaved contrary to expectation based on oxygen saturation alone, suggesting that other factors influence their distributions, for example damselflies in the family Coengriidae were negatively associated with *E. nuttallii*, leeches in the family Glossiphonidae were positively associated with *E. nuttallii*, and freshwater snails in the genera *Hippeautis*, *Lymnea*, *Valvata*, *Physa* and *Bithynia*, which have similar oxygen requirements, show a range of different responses. Allelopathy may explain observed negative association between *E. nuttalii* and lepidopteran larvae in the family Pyralidae, as *E. nuttalii* has been previously shown to retard the growth and reduce the survival of the Pyralidae species *Acentria ephemerella* under laboratory conditions (Erhard et al. 2007). Where Pyralidae larvae exist in large numbers they may substantially reduce cover of other macrophyte species providing an indirect advantage to *Elodea* spp. (Gross et al. 2001).

One weakness of the pairing of native and invasive plant beds in this study was that it was not possible to use sites where only *E. nuttallii* was present (i.e. highly invaded sites). Therefore, if native species are required at particular points in invertebrate life cycles (e.g. reproduction), population declines associated with their absence may not have been detected as invertebrate species could move between plant beds if necessary. Additionally, many Northern Irish water bodies, such as those sampled here, have been subject to considerable

pressure from eutrophication, pollution and human disturbance, especially in lowland areas (Heegaard et al. 2001) prior to the introduction of invasive species, such as *E. nuttallii*. The algal and invertebrate communities present in these waterbodies differ from those in more pristine sites, especially in the relative lack of rare species. Impacts of invasive macrophytes may also differ depending on trophic status of waterbodies (Strayer 2010) and in some cases the same invasive macrophyte species has opposite effects on invertebrates in different study systems (Schultz, Dibble 2012). Therefore, it is possible that the impact of *E. nuttallii* on invertebrate and algal communities would have been different in oligotrophic sites or more pristine sites which had not been previously impacted by anthropogenic pressures.

Together these field studies provide insights into the potential impacts of the widespread invader *Elodea nuttallii* on a range of taxa in temperate waterbodies. Due to the correlational nature of these studies it is not possible to determine cause-and-effect or to reveal the exact drivers of change in biological communities. Here, where possible we have used closely paired sites within waterbodies to minimise potentially confounding differences between sites. We suggest that the results of this research may be used to direct further research including both field and laboratory experiments focused on the interaction of *E. nuttallii* with particular species of concern (e.g. the observed negative association of *E. nuttallii* and charophytes).

In conclusion, our findings suggest that whilst *E. nuttallii* significantly altered freshwater communities, observed differences were small relative to other factors such as nutrient levels, inter-annual variation and differences between sites. In addition, we add to a growing body of literature that suggests that the impacts of aquatic invasive plant species are not consistently negative and they may, for example, increase the richness of native plant species or the abundance of invertebrate species if total plant biomass increases as a result of invasion (Schultz, Dibble 2012; Strayer 2010; Thomaz et al. 2012).

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783

Tables

Table 1. Results of partial Canonical Correspondence Analysis (pCCA) of macrophyte structural groups, showing orthogonal species scores when *Elodea nuttallii* is fitted as the explanatory variable and quadrat and year are accounted for by partial CCA; variance explained by percentage cover of *Elodea nuttallii*, variance explained by year and the variance explained by the full model (i.e. *Elodea nuttallii*, year and quadrat).

	CCA scores against only *Elodea nuttallii*	**Variance explained by *Elodea nuttallii* (%)**	**Variance explained by year (%)**	**Variance explained by full model (%)**
Submersed low-growing	-0.60	0.25	0.45	52.70
Charophytes	-0.28	0.50	10.55	63.50
Emergent	-0.16	1.12	0.67	87.12
Filamentous algae	0.04	0.13	3.80	88.26
Submersed canopy-forming	0.04	0.15	4.57	89.21
Bryophytes	0.17	0.06	1.41	74.78
Floating-rooted species	0.43	0.96	0.41	48.18
Free-floating	0.47	1.77	2.98	79.45

791

792 **Table 2.** Results of partial Canonical Correspondence Analysis (pCCA) for the genera most
793 strongly associated with *Elodea nuttallii*. Genera with greater than 0.5% of variation
794 explained by *Elodea nuttallii* are shown. Table shows species from each genus present in the
795 dataset, species scores when *Elodea nuttallii* is fitted as the explanatory variable and depth,
796 quadrat location and year are accounted for by partial CCA, variance explained by percentage
797 cover of *Elodea nuttallii*, variance explained by depth and year, and the variance explained
798 by the full model.

799

Genus/Family	**Species**	**CCA scores against only *Elodea nuttallii***	**Variance explained by *Elodea nuttallii* (%)**	**Variance explained by depth and year (%)**	**Variance explained by full model (%)**
Elodea	*E. canadensis*	-0.77	3.01	4.12	74.99
Juncus	*J. bulbosus*	-0.65	0.80	4.08	61.64
Sparganium	*S. emersum* *S. erectum*	-0.32	0.54	0.57	69.87
**Characeae*	*Chara globularis* *Chara vulgaris* *Nitella flexilis agg.* *Nitella translucens*	-0.32	0.65	10.68	63.77
Equisetum	*E. fluviatile* *E. palustre*	-0.30	0.68	5.55	77.02
Potamogeton	*P. alpina* *P. crispus* *P. filiformis* *P. friesii* *P. lucens* *P. natans* *P. obtusifolius* *P. pectinatus* *P. perfoliatus* *P. praelongus* *P. pusillus* *P. trichoides* *P. zizii*	0.10	0.67	2.16	89.54
Nuphar	*N. lutea*	0.44	0.94	1.25	47.75
Nymphaea	*N. alba*	0.94	0.54	2.63	45.54
Stratiotes	*S. aloides*	1.60	4.75	8.16	73.69

* Characeae were analysed at a family level as 2006 and 2007 surveys did not record at a species level within this family

800 **Table 3.** Results of partial Canonical Correspondence Analysis (pCCA) of invertebrate taxa
801 living on macrophytes in lakes. Taxanomic groups which were present in more than one
802 sample and for which > 0.5% of variation is explained by *Elodea nuttallii* are shown. Table
803 details taxa scores when *Elodea nuttallii* is fitted as the explanatory variable, variance
804 explained by percentage cover of *Elodea nuttallii*, and the variance explained by the full
805 model.
806

Taxa	**Species present**	**Order**	**CCA scores against *Elodea nuttallii* only**	**Variance explained by *Elodea nuttallii* (%)**	**Variance explained by full model (%)**
Pyralidae	Spp.	Lepidoptera	-2.21	27.29	32.27
Hydrachna	Spp.	Trombidiformes	-1.47	17.93	57.90
Coenagrionidae	Spp.	Odonata	-1.27	5.47	9.03
Erpobdella	*E. octoculata* *E. testacea*	Rhynchobdellida	-1.25	20.00	55.60
Chironomidae	Spp.	Diptera	-1.16	38.42	45.23
Rhyacophila	Spp.	Trichoptera	-0.92	0.65	37.26
Physa	*P. fontinalis*	*Planorboidea	-0.74	5.01	17.72
Lymnaea	*L. auricularia* *L. palustris* *L. peregra*	Lymnaea	-0.70	6.23	33.01
Gyraulus	*G. albus*	*Planorboidea	0.34	1.25	24.87
Crangonyx	*C. pseudogracilis*	Amphipoda	0.37	1.70	17.04
Sialis	*S. lutaria*	Megaloptera	0.77	2.56	46.89
Bithynia	*B. tentaculata*	*Truncatelloidea	0.98	8.56	49.57
Cortixinae	Spp.	Hemiptera	1.22	9.30	49.01
Valvata	*V. cristata,* *V. piscinalis*	*Valvatoidea	1.94	11.46	33.69
Limnephilidae	Spp.	Trichoptera	2.03	26.19	45.12
Hippeutis	*H. complanatus*	Gastropoda	2.05	11.73	31.97
Pisidium	*P. casertanum* *P. subtruncatum*	*Planorboidea	2.44	23.66	54.02

* within the class Gastropoda, superfamily is given instead of Order as Orders are not defined for these taxa
807
808

809 **Table 4.** Results of partial Canonical Correspondence Analysis (pCCA) of invertebrate taxa
810 living on macrophytes in rivers. Taxonomic groups which were present in more than one
811 sample and for which > 0.5% of variation is explained by *Elodea nuttallii* are shown. Table
812 details taxa scores when *Elodea nuttallii* is fitted as the explanatory variable, variance
813 explained by percentage cover of *Elodea nuttallii*, and the variance explained by the full
814 model.
815

Taxa	Species present	Order	CCA scores against Elodea nuttallii only	Variance explained by Elodea nuttallii (%)	Variance explained by full model (%)
Crangonyx	*C. pseudogracilis*	Amphipoda	-3.07	40.46	55.82
Sialis	*S. lutaria*	Megaloptera	-2.78	37.99	52.11
Bithynia	*B. tentaculata*	*Truncatelloidea	-1.88	29.44	55.33
Pisidium	*P. amnicum* *P. casertanum*	Veneroida	-1.81	6.49	13.26
Theromyzon	*T. tessulatum*	Rhynchobdellida	-1.66	9.72	52.30
Haliplus	*H. confinis*	Coleoptera	-1.29	7.74	59.27
Stictotarsus	*S. duodecimpustulatus*	Coleoptera	-1.18	6.94	61.61
Coenagrionidae	Spp.	Odonata	-0.89	1.12	16.89
Asellus	*A. aquaticus*	Amphipoda	-0.59	14.33	57.41
Physa	*P. fontinalis*	*Planorboidea	-0.44	3.23	57.12
Chironomidae	spp.	Diptera	-0.36	1.24	13.24
Helobdella	*H. stagnalis*	Rhynchobdellida	-0.29	3.75	64.28
Lymnaea	*L. palustris* *L. stagnalis* *L. peregra* *L. trunculata*	*Lymnaeoidea	-0.26	1.32	81.69
Cortixinae	Spp.	Hemiptera	0.67	1.89	32.35
Valvata	*V. piscinalis*	*Valvatoidea	0.85	1.91	28.78
Gyraulus	*G. albus*	*Planorboidea	0.87	5.58	72.10
Gammarus	*G. pulex*	Amphipoda	0.97	5.26	25.61
Planorbis	*P. carinatus*	*Planorboidea	1.19	22.78	60.58
Planorbarius	*P. corneus*	*Planorboidea	1.28	20.42	75.93
Notonecta	Spp.	Hemiptera	1.28	9.16	17.87
Limnephilidae	Spp.	Trichoptera	1.28	8.45	64.97
Glossiphonia	*G. complanata* *G. heteroclite*	Rhynchobdellida	2.28	20.12	40.63
Hippeutis	*H. complanatus*	*Planorboidea	2.69	14.39	38.29

* within the class Gastropoda, superfamily is given instead of Order as Order is not defined for these taxa

816

Figures & legends

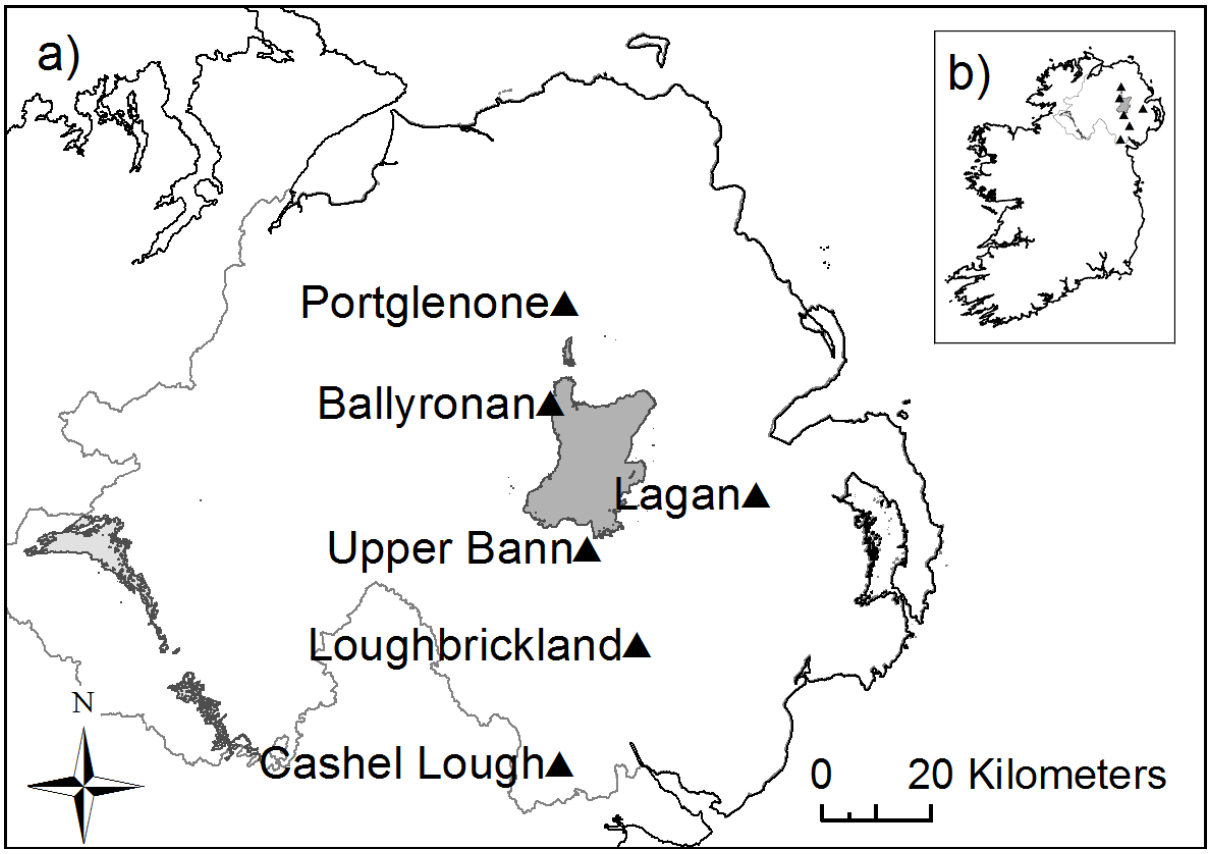
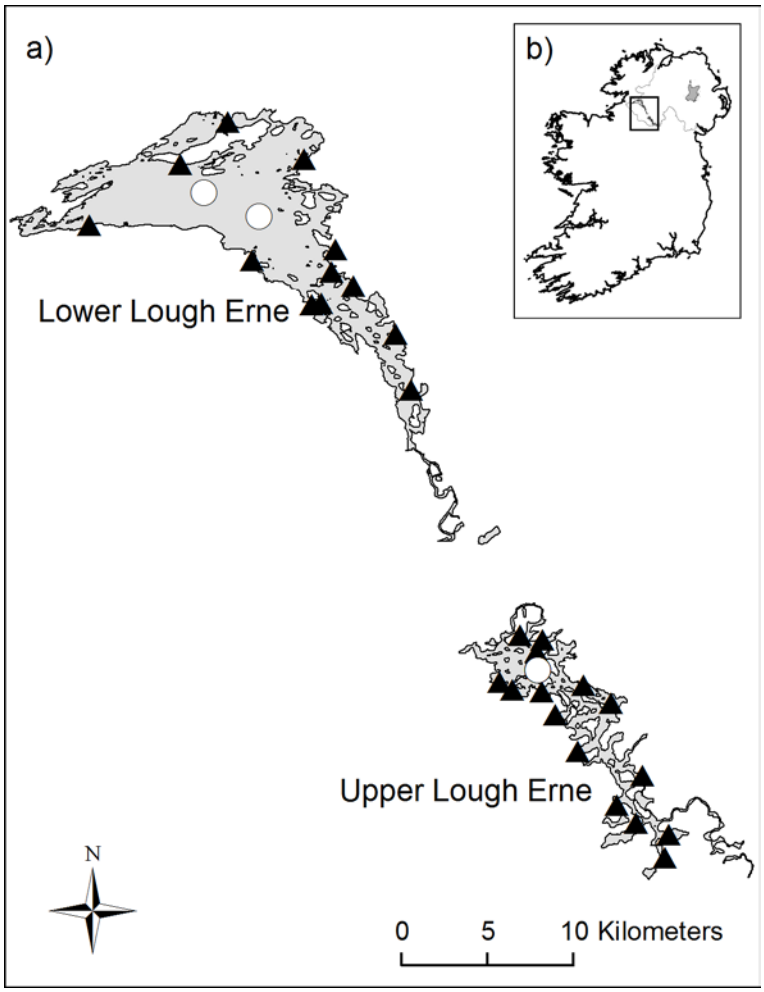


Fig. 1 a) Field sites for study of impacts of *Elodea nuttallii* on dissolved oxygen, chorophyll *a*, pH, algae and invertebrates. Samples were paired within sites such that samples were taken from a stand of *E. nuttallii* and a stand of native plants within each site, b) inset map of Ireland showing field site locations.



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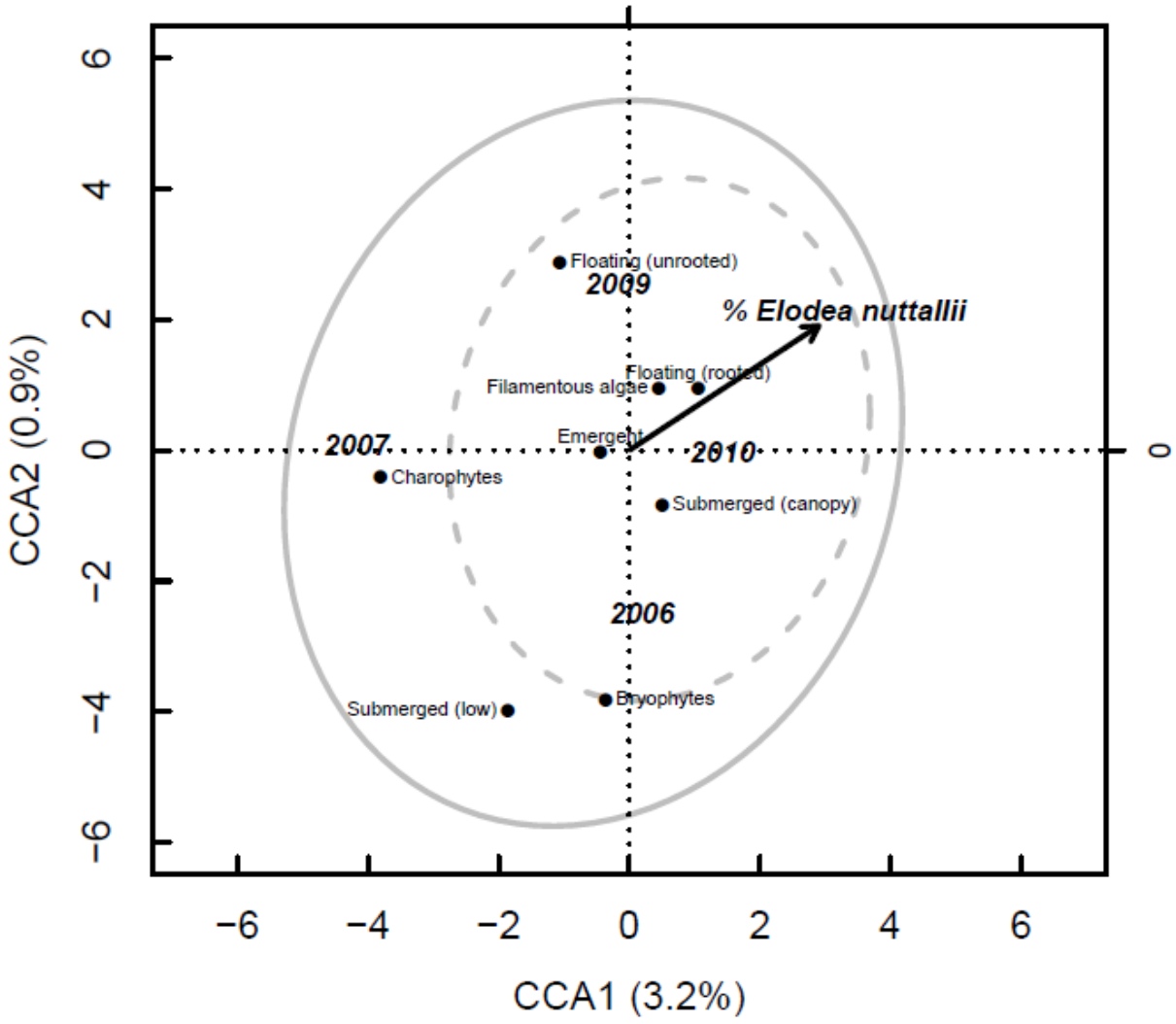
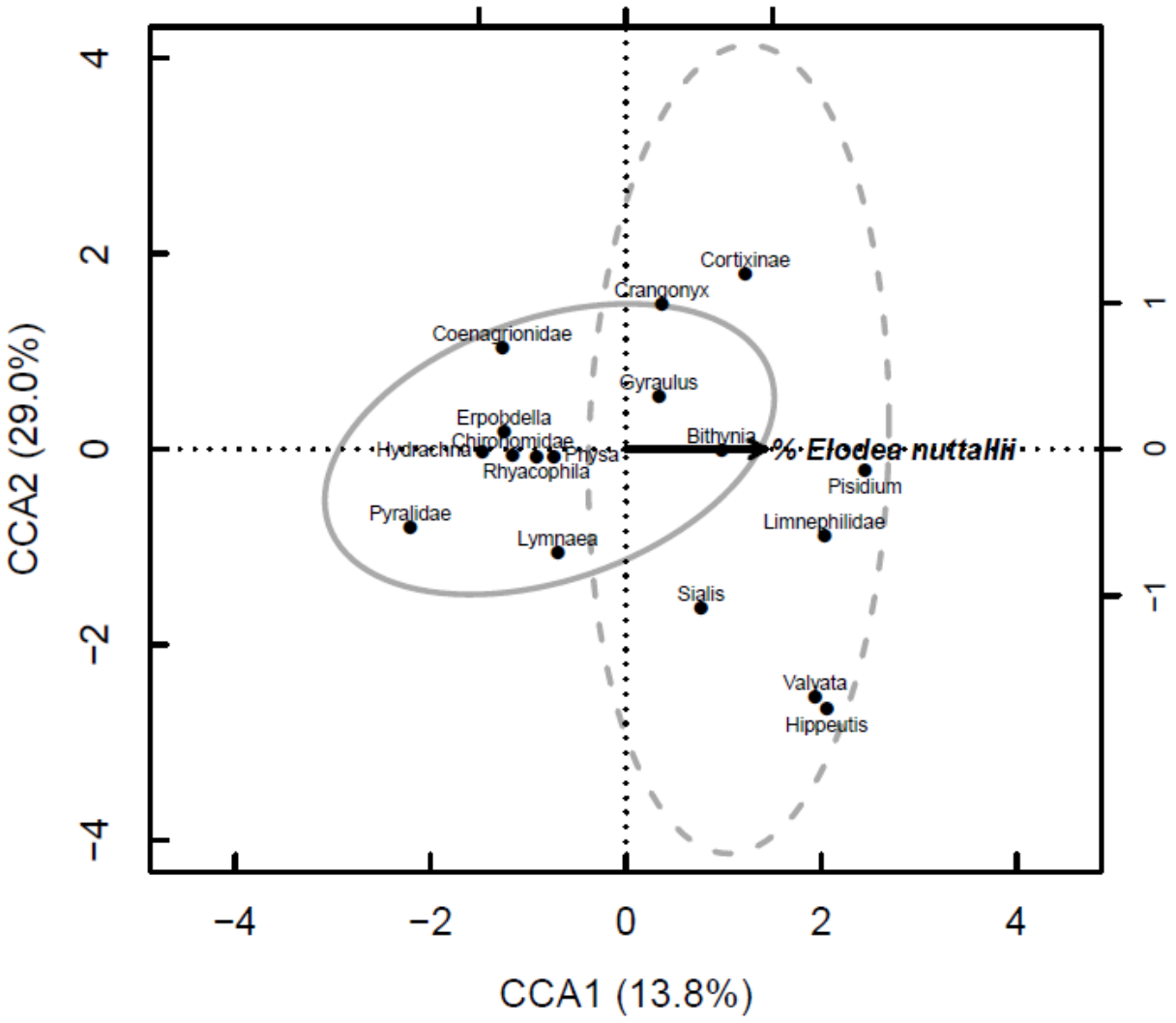
825

826 **Fig. 2** a) Study sites for macrophytes in Lough Erne. Black triangles show the locations of
827 survey transects. White circles show locations where water chemistry parameters were
828 measured, b) inset map of Ireland showing location of Lough Erne.



829

830 **Fig. 3** Plot of partial Canonical Correspondence Analysis showing relationships between
831 *Elodea nuttallii* and plant functional groups, when year is also fitted an explanatory factor
832 and quadrat ID is accounted for as a random factor. Species scores are unscaled. Axis labels
833 show % of total variation in macrophyte communities explained by each CCA axis. Grey
834 ellipse shows 95% confidence interval around sites where *Elodea nuttallii* is present, dashed
835 grey ellipse shows 95% confidence interval around sites where *Elodea nuttallii* is not present.



836

837 **Fig. 4** Plot of partial Canonical Correspondence Analysis showing relationships between
838 *Elodea nuttallii* and invertebrate taxa in lakes, when site is accounted for as a random factor.
839 Species scores are unscaled. Taxonomic groups which were present in more than one sample
840 and for which > 0.5% of variation is explained by *Elodea nuttallii* are shown. Axis labels
841 show % of total variation in macrophyte communities explained by each CCA axis. Grey
842 ellipse shows 95% confidence interval around sites where *Elodea nuttallii* is present, dashed
843 grey ellipse shows 95% confidence interval around sites where *Elodea nuttallii* is not present.

844

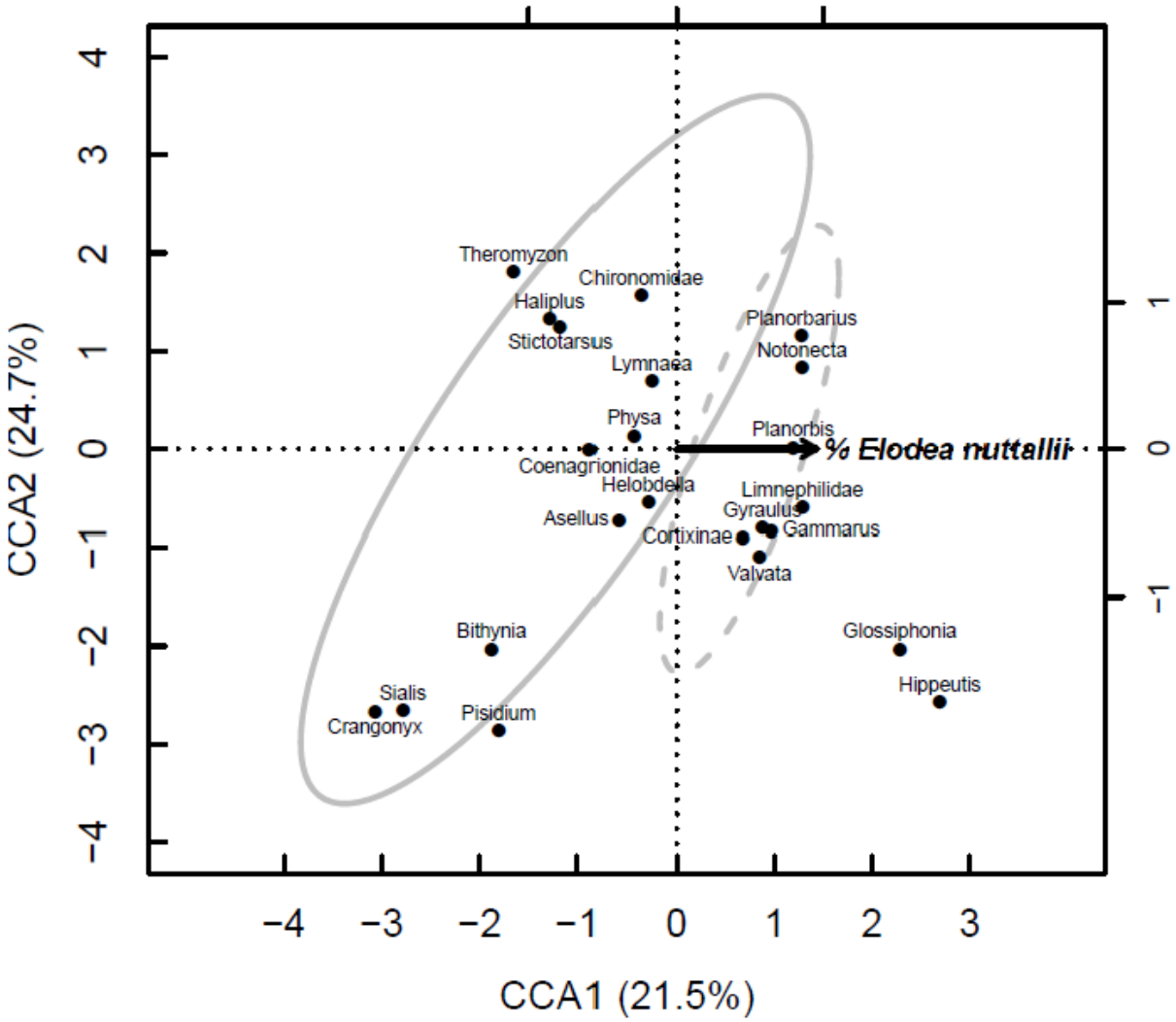


Fig. 5 Plot of partial Canonical Correspondence Analysis showing relationships between *Elodea nuttallii* and invertebrate taxa in rivers, when site is accounted for as a random factor. Species scores are unscaled. Taxonomic groups which were present in more than one sample and for which > 0.5% of variation is explained by *Elodea nuttallii* are shown. Axis labels show % of total variation in macrophyte communities explained by each CCA axis. Grey ellipse shows 95% confidence interval around sites where *Elodea nuttallii* is present, dashed grey ellipse shows 95% confidence interval around sites where *Elodea nuttallii* is not present.

Supplementary material

Table S1 Algal functional groups used

Table S2 Invertebrate biomass regression models

Table S3 Invertebrate feeding guilds

Table S4 Macrophyte structural groups

Table S5 Model details of macrophyte GLMMs

Table S6 Model details of macrophyte pCCAs

Table S7 Model details of GLMMs of dissolved oxygen, chorophyll *a*, pH and plant biomass.

Table S8 Model details of algae GLMMs

Table S9 Model details of algae pCCAs

Table S10 Model details of invertebrate GLMMs

Table S11 Model details of invertebrate pCCAs

Table S12 Model details for multivariate analyses of homogeneity.

Supplementary material

Table 1 Algal functional groups. Table shows which taxonomic groups were placed in each functional group for analysis.

Group	Key morphological features	Taxonomic group
1	Small organisms with high surface/volume ratio	*Lyngbya*, *Oscillatoria*, picoplankton, *Stichococcus*
2	Small, flagellated, with siliceous exoskeletal features	*Chromulina*, *Chrysophyta*, *Synura*
3	Large filaments with aerotopes	*Anabaena spiroides*, *Chroococcales*, *Hapalosiphon*, *Nostoc*
4	Medium size organisms, lacking specialised traits	*Ankyra*, *Aphanochaete magna*, *Bumilleriopsis*, *Characiochloris*, *Characiopsis*, *Characium*, *Closteriopsis acicularis*, *Closterium*, *Cosmarium*, *Microthamnion kuetzingianum*, *Monoraphidium*, *Mougeotia*, *Netrium*, *Oedogonium*, *Ophiocytium*, *Pediastrum duplex*, *Pediastrum tetras*, *Scenedesmus*, *Tetraedron*, *Tetrastrum staurogeniaeforme*, *Treubaria*
5	Medium to large flagellates	*Chlamydomonas*, *Chroomonas*, *Cryptomonas*, Dinophyceae *Euglena*, *Gymnodinium*, *Haematococcus*, *Katodinium*, *Pandorina morum*, *Phacus*, *Trachelomonas*
6	Non-flagellates with siliceous exoskeletons	*Achnanthes*, *Achnanthidium*, *Amphora*, *Aulacoseira* *Cocconeis*, *Cyclotella*, *Cymbella*, *Denticula*, *Diadesmis*, *Encyonema*, *Epithemia*, *Eunotia*, *Fragilaria*, *Frustulia*, *Gomphonema*, *Gyrosigma*, *Melosira varians*, *Meridion*, *Navicula*, *Nitzschia*, *Pinnularia*, *Pseudostaurosira*, *Rhoicosphenia curvata*, *Staurosirella*, *Stephanodiscus*, *Surirella*
7	Large mucilaginous colonies	*Chamaesiphon*, Chlorococcales, *Gomphosphaeria*, *Hydrococcus*, *Kirchneriella obesa*, *Lagerheimia genevensis*, *Merismopedia*, *Microcystis*, *Oscillatoria*, *Phormidium*, *Protoderma*, *Quadrigula*, *Radiococcus*, *Rhabdoderma*
8	Uncategorised genera	Unidentifiable genera

Table S2 Best fitting invertebrate biomass regression models and formulae. Optimal regressions based on width/length (mm) and biomass (mg) of invertebrate taxa.

Invertebrate Taxa	***n***	***p***	**Adj R^2**	**Intercept (SE)**	**Slope (SE)**	**X variable + tranformation**
Asellidae	162	<0.001	0.70	-5.07 (0.25)	2.67 (0.14)	Length (Ln)
Bithyniidae	57	<0.001	0.80	-2.59 (0.29)	2.01 (0.13)	Length (Ln)
Chironomus	29	<0.001	0.62	-4.18 (0.68)	1.67 (0.24)	Length (Ln)
Erpobdellidae	15	<0.001	0.92	-9.17 (0.72)	3.22 (0.25)	Length (Ln)
Glossiphonidae	24	0.0402	0.13	-1.82 (0.64)	0.63 (0.29)	Length (Ln)
Hydrobiidae	156	<0.001	0.40	-3.36 (0.22)	1.75 (0.17)	Length (Ln)
Lymnaeidae	81	<0.001	0.72	-3.76 (0.35)	2.59 (0.18)	Length (Ln)
Physidae	6	<0.001	0.85	-2.77 (0.64)	2.00 (0.37)	Length (Ln)
Planorbidae	24	<0.001	0.72	-1.23 (0.18)	2.06 (0.27)	Width (Log_{10})
Sphaeriidae	18	<0.001	0.74	-4.55 (0.56)	2.54 (0.35)	Width (Ln)
Valvatidae	52	<0.001	0.69	-3.41 (0.27)	2.75 (0.25)	Width (Ln)

Table S3 Invertebrate feeding guilds. Table shows which taxonomic groups were placed in each feeding guild for analysis.

Collector Filterer	**Collector Gatherer**	**Herbivore Piercer**	**Predator**	**Scraper Grazer**	**Shredder**
Chydoridae	*Baetidae*	Corixinae	*Argyroneta*	*Asellus*	Chrysomelidae
Culicidae	*Beraea*	Curculionidae	*Batracobdella*	*Bithynia*	Elminthidae
Cyclopoida	*Caenis*	*Donacia*	Chaoboridae	*Brychius*	*Gammarus*
Daphniidae	*Dicrotendipes*	*Macroplea*	Coenagrionidae	*Crangonyx*	*Helophorus*
Pisidium	*Endochironomus*		Dytiscidae	*Gyraulus*	Pyralidae
Polycentropodidae	Chironomidae		*Erpobdella*	Haliplidae	*Glyptotendipes*
Microtendipes	*Chironomus*		*Gerris*	*Haliplus*	*Polypedilum*
	Limnephilidae		*Glossiphonia*	*Hippeutis*	
	Oligochaeta		*Helobdella*	*Lymnaea*	
			Hydrachna	*Physa*	
			Limnesia	*Planorbarius*	
			Nepidae	*Planorbis*	
			Notonecta	*Potamopyrgus*	
			Rhyacophila	*Valvata*	
			Sialis		
			Stictotarsus		
			Theromyzon		
			Velia		

Table S4 Macrophyte structural groups. Table shows which taxonomic groups were placed in each structural group for analysis.

Structural group	Taxonomic group
Emergent	*Alisma lanceolatum, Alisma plantago-aquatica, Apium inundatum, Baldellia ranunculoides, Butomus umbellatus, Caltha palustris, Carex rostrata, Carex vesicaria, Cicuta virosa, Eleocharis palustre, Epilobium hirsutum, Equisetum fluviatile, Equisetum palustre, Filipendula ulmaria, Glyceria fluitans, Iris pseudacorus, Juncus bulbosus, Lythrum spp., Mentha aquatica, Menyanthes trifoliata, Myosotis scorpioides, Phalaris arundinacea, Phragmites australis, Persicaria amphibia, Potentilla palustris, Ranunculus flammula, Schoenoplectus spp., Solanum dulcamara, Sparganium erectum, Stachys palustris, Typha latifolia*
Free-floating	*Hydrocharis morsus-ranae, Lemna gibba, Lemna minor, Lemna minuta, Lemna polyrhiza, Lemna trisulca, Stratiotes aloides*
Floating rooted	*Nuphar lutea, Nymphaea alba, Potamogeton natans, Sagittaria sagittifolia*
Submersed, canopy forming	*Callitriche spp., Callitriche hamulata, Ceratophyllum demersum, Elodea canadensis, Elodea nuttallii, Myriophyllum alternifolium, Myriophyllum spicatum, Potamogeton alpina, Potamogeton crispus, Potamogeton filiformis, Potamogeton friesii, Potamogeton gramineus Potamogeton lucens, Potamogeton obtusifolius, Potamogeton pectinatus, Potamogeton perfoliatus, Potamogeton praelongus, Potamogeton pusillus, Potamogeton trichoides, Potamogeton gramineus x lucens, Ranunculus penicillatus, Ranunculus circinatus, Sparganium emersum, Zannichella palustre*
Submersed, low growing	*Eleocharis acicularis, Isoetes spp., Littorella uniflora*
Bryophytes	*Fontinalis antipyretica, Fontinalis squamosa, Scapania spp.*
Filamentous algae	Chlorophyta
Charophytes	Charophyceae

Table S5. Univariate models of macrophyte cover and species richness, where quadrat nested within lake was fitted as a random factor. "na" indicates variables not included in the final model.

Model/explanatory variables	β ± s.e.	Wald χ^2	p
a) % macrophytes cover ($\chi^2_{df=717}$ = 180.88, p<0.001)			
% *Elodea nuttallii*	0.013 ± 0.003	20.24	<0.001
% *Elodea canadensis*	0.029 ± 0.012	5.53	0.019
Depth	-0.470 ± 0.083	31.90	<0.001
Year	Factorial	8.47	0.037
Nutrient concentration	-3.690 ± 2.109	3.06	0.080
% *E. nuttallii* * % *E. canadensis*	na		
b) % native macrophytes cover ($\chi^2_{df=719}$ = 101.74, p<0.001)			
% *Elodea nuttallii*	na	na	na
% *Elodea canadensis*	na	na	na
Depth	-0.494 ± 0.087	32.42	<0.001
Year	Factorial	9.51	<0.001
Nutrient concentration	-4.082 ± 2.214	3.40	0.065
% *E. nuttallii* * % *E. canadensis*	na		
c) % native macrophyte richness ($\chi^2_{df=717}$ =, p<0.001)			
% *Elodea nuttallii*	0.002 ± 0.001	3.85	0.050
% *Elodea canadensis*	0.013 ± 0.004	11.58	
Depth	-0.397 ± 0.043	88.77	
Year	Factorial	26.86	
Nutrient concentration	3.407 ± 1.176	8.39	0.004
% *E. nuttallii* * % *E. canadensis*	na		

Table S6. Results of pCCA models of cover of macrophyte genera and cover of macrophyte structural groups, where quadrat is accounted for as a conditional factor. "na" indicates variables which were not included in the final model.

Model/explanatory variables	Variance explained (%)	p
a) % cover of macrophyte genera (df = 697, Conditional variance (Site) = 53.9, Constrained variance = 3.9, p = 0.010)		
% *Elodea nuttallii*	0.5	0.005
% *Elodea canadensis*	na	na
Depth	0.5	0.005
Year	2.0	0.005
Nutrient concentration	na	na
% *E. nuttallii* * % *E. canadensis*	na	na
b) % cover of structural groups (df = 361, Conditional variance (Site) = 69.0, Constrained variance = 4.6, p = 0.005)		
% *Elodea nuttallii*	0.6	0.005
% *Elodea canadensis*	na	na
Depth	na	na
Year	2.7	0.005
Nutrient concentration	na	na
% *E. nuttallii* * % *E. canadensis*	na	na

Table S7. Results of univariate models of dissolved oxygen, chlorophyll *a*, pH, and plant biomass where site is fitted as a random factor. "na" indicates variables not included in the final model.

Model/explanatory variables	***β* ± s.e.**	**Wald χ^2**	***p***
a) dissolved oxygen saturation ($\chi^2_{df=31}$ = 6.25, p=0.043)			
Elodea nuttallii	Factorial	3.21	0.073
Month	na	na	na
Nutrient concentration	na	na	na
Nutrient concentration * *E. nuttalii*	na	na	na
River/Lake	Factorial	4.23	0.040
River/Lake * *E. nuttallii*	na	na	na
b) chlorophyll *a* ($\chi^2_{df=34}$ = 1.61, p=0.204)			
Elodea nuttallii	na	na	na
Month	na	na	na
Nutrient concentration	na	na	na
Nutrient concentration * *E. nuttalii*	na	na	na
River/Lake	na	na	na
River/Lake * *E. nuttallii*	na	na	na
c) pH ($\chi^2_{df=33}$ =40.45, p<0.001)			
Elodea nuttallii	na	na	na
Month	Factorial	125.69	<0.001
Nutrient concentration	na	na	na
Nutrient concentration * *E. nuttalii*	na	na	na
River/Lake	na	na	na
River/Lake * *E. nuttallii*	na	na	Na
d) plant biomass ($\chi^2_{df=23}$ =1.99, p = 0.158)			
Elodea nuttallii	na	na	na
Month	na	na	na
Nutrient concentration	na	na	na
Nutrient concentration * *E. nuttalii*	na	na	na
River/Lake	na	na	na
River/Lake * *E. nuttallii*	na	na	na

Table S8. Results of univariate models of algal biovolume and richness of algal taxa, where site is fitted as a random factor. "na" indicates variables which were not included in the final model.

Model/explanatory variables	β ± s.e.	Wald χ^2	*p*
a) algal biovolume ($\chi^2_{df=29}$ = 7.32, *p*=0.026)			
Elodea nuttallii	na	na	na
Month	Factorial	8.40	0.015
Nutrient concentration	na	na	na
Nutrient concentration * *E. nuttalii*	na	na	na
River/Lake	na	na	na
River/Lake * *E. nuttallii*	na	na	na
b) richness of algal taxa ($\chi^2_{df=27}$ = 177.68, *p*<0.001)			
Elodea nuttallii	na	3.67	0.055
Month	na	20.19	<0.001
Nutrient concentration	na	na	na
Nutrient concentration * *E. nuttalii*	na	na	na
River/Lake	na	na	na
River/Lake * *E. nuttallii*	na	na	na

Table S9. Results of pCCA models of algal taxa and algal functional groups, where site is accounted for as a conditional factor. "na" indicates variables which were not included in the final model.

Model/explanatory variables	Variance explained (%)	*p*
a) biovolume of algal taxa		
(df = 23, Conditional variance(Site) = 34.5, Constrained variance = 15.5, *p* = 0.015)		
Elodea nuttallii	na	na
Month	7.1	0.041
Nutrient concentration	5.3	0.030
Nutrient concentration**E.nuttallii*	na	na
River/Lake	na	na
River/Lake * *E. nuttallii*	na	na
b) biovolume of functional groups		
(df = 25, Conditional variance(Site) = 19.1, Constrained variance = 0, *p* = 0.340)		
Elodea nuttallii	na	na
Month	na	na
Nutrient concentration	na	na
Nutrient concentration**E.nuttallii*	na	na
River/Lake	na	na
River/Lake * *E. nuttallii*	na	na

Table S10. Results of univariate models of invertebrate biomass and richness, where site is fitted as a random factor. "na" indicates variables which were not included in the final model.

Model/explanatory variables	β ± s.e.	Wald χ^2	p
a) biomass of invertebrates on macrophytes ($\chi^2_{df=18}$ = 20.87, p<0.001)			
Elodea nuttallii	na	na	na
Month	Factorial	12.05	<0.001
Nutrient concentration	0.561 ± 0.200	7.85	<0.001
Nutrient concentration * *E. nuttalii*	na	na	na
Plant density	0.495 ± 0.120	17.01	< 0.001
River/Lake	na	na	na
River/Lake * *E. nuttallii*	na	na	na
b) richness of invertebrates on macrophytes ($\chi^2_{df=21}$ = 13.33, p=0.002)			
Elodea nuttallii	na	na	na
Month	Factorial	6.30	0.012
Nutrient concentration	na	na	Na
Nutrient concentration * *E. nuttalii*	na	na	Na
Plant density	0.125 ± 0.075	2.76	0.096
River/Lake	na	na	na
River/Lake * *E. nuttallii*	na	na	na
c) biomass of invertebrates in sediment ($\chi^2_{df=20}$ =8.93, p<0.001)			
Elodea nuttallii	na	na	na
Month	na	na	na
Nutrient concentration	0.792 ± 0.341	9.54	0.002
Nutrient concentration * *E. nuttalii*	na	na	na
Plant density	na	na	na
River/Lake	na	na	na
River/Lake * *E. nuttallii*	na	na	na
d) richness of invertebrates in sediment ($\chi^2_{df=20}$ =1.99, p = 0.158)			
Elodea nuttallii	na	na	na
Month	na	na	na
Nutrient concentration	na	na	na
Nutrient concentration * *E. nuttalii*	na	na	na
Plant density	na	na	na
River/Lake	na	na	na
River/Lake * *E. nuttallii*	na	na	na

Table S11. Results of pCCA models of invertebrate taxa and feeding guilds, where site is accounted for as a conditional factor. "na" indicates variables which were not included in the final model.

Model/explanatory variables	Variance explained (%)	*p*
a) biomass of invertebrate taxa on macrophytes (df = 15, Conditional variance(Site) = 39.9, Constrained variance = 0, *p*=0.017)		
Elodea nuttallii	na	na
Month	na	na
Nutrient concentration	na	na
Nutrient concentration**E.nuttallii*	na	na
Plant density	na	na
River/Lake	na	na
River/Lake * *E. nuttallii*	na	na
b) biomass of invertebrate feeding guilds on macrophytes (df = 17, Conditional variance(Site) = 45.2, Constrained variance = 10.5, *p*=0.005)		
Elodea nuttallii	na	na
Month	na	na
Nutrient concentration	na	na
Nutrient concentration**E.nuttallii*	na	na
Plant density	na	na
River/Lake	na	na
River/Lake * *E. nuttallii*	10.45	0.044
c) biomass of invertebrate taxa in sediment (df = 17, Conditional variance(Site) = 42.4, Constrained variance = 0, *p*=0.005)		
Elodea nuttallii	na	na
Month	na	na
Nutrient concentration	na	na
Nutrient concentration**E.nuttallii*	na	na
Plant density	na	na
River/Lake	na	na
River/Lake * *E. nuttallii*	na	na
c) biomass of invertebrate taxa in sediment (df = 17, Conditional variance(Site) = 42.4, Constrained variance = 0, *p*=0.005)		
Elodea nuttallii	na	na
Month	na	na
Nutrient concentration	na	na
Nutrient concentration**E.nuttallii*	na	na
Plant density	na	na
River/Lake	na	na
River/Lake * *E. nuttallii*	na	na

Table S12. Results of analyses of multivariate homogeneity of group dispersion for macrophyte, algae and invertebrate taxa. Estimates show mean Jaccard dissimilarity between sites with *E. nuttallii* present and mean Jaccard dissimilarity between sites without *E. nuttallii*, based on presence and absence of taxa.

Model/explanatory variables	**mean ± se**
a) macrophyte taxa ($F_{df=726}$ =24.34, p<0.001)	
Elodea nuttallii present	0.43 ± < 0.01
Elodea nuttallii absent	0.49 ± < 0.01
b) algal taxa($F_{df=24}$ =0.42, p=0.521)	
Elodea nuttallii present	0.49 ± < 0.01
Elodea nuttallii absent	0.48 ± 0.02
c) invertebrate taxa on macrophytes ($F_{df=22}$ =0.92, p=0.179)	
Elodea nuttallii present	0.55 ± 0.03
Elodea nuttallii absent	0.60 ± 0.03
d) invertebrate taxa in sediment ($F_{df=22}$ =0.92, p=0.179)	
Elodea nuttallii present	0.51 ± 0.02
Elodea nuttallii absent	0.53 ± 0.03